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Modelling photosynthetic light-response curve in *Calotropis procera* under salinity or water deficit stress using non-linear models

Abdellah Akhkha

Biology Department, Faculty of Science, Taibah University, AlMadinah AlMunawwarah, Kingdom of Saudi Arabia

Abstract
In the present study, the photosynthetic light-response curves (PLR curves) of the wild shrub *Calotropis procera* were determined under water deficit or salinity stressed plants. The Thornley and Marshall & Biscoe non-linear models were tested in order to investigate which model better describes the photosynthetic light-response curve. When no constraints were exerted on dark respiration values, Thornley model was a better fit. However, when the measured dark respiration values were forced into the model, the PLR curve fits well to Marshall & Biscoe model. The latter gave more pronounced effects of water deficit or salinity stress on the PLR curve parameters such as maximum gross photosynthesis *Pgmax*, apparent quantum efficiency α and the convexity θ of the curve. The features of both above mentioned mathematical models to describe the photosynthetic light-response curve of Calotropis plant are discussed.

Keywords: Apparent quantum efficiency, convexity, non-linear model, photosynthetic light-response curve, salinity stress, water stress.

Corresponding auther : abdellah99@gmail.com
Tel :0096530175197 Fax: 0096648454770.

1. Introduction

Different models have been proposed to describe the photosynthetic light-response curve (PLR curve). Blackman [1] derived one of the earliest models, which describes a response of photosynthesis that increases linearly with irradiance (light-limited) until the CO_2 supply becomes limiting (CO_2-limited). This model is inadequate, because the PLR curve shows sharp discontinuity between the light-limited and CO_2-limited regions. For these reasons, other models were proposed. A later model proposed by Rabinowich [2] describes the relationship between photosynthesis and irradiance in terms of a rectangular hyperbola. This model, known also as the linear model, was derived from the *Michaelis-Menten* relation between the rate of an enzyme-catalysed reaction and the concentration of its substrate [3]. It defines two parameters, P_{max} the maximum (gross or net) photosynthesis rate and the quantum efficiency (α). The linear model can also be used to estimate a third parameter, dark respiration (*Rd*).

However, this model has been shown to be a poor description of the PLR curve at certain saturating levels of CO_2 by some workers [4 , 5, 6] . Working with the flag leaf of winter wheat, Marshall and Biscoe [7] demonstrated that the linear model over estimates the quantum efficiency (α), the maximum rate of photosynthesis (P_{max}) and dark respiration (*Rd*), and underestimates the rate of photosynthesis at the intermediate light-levels (100-500 μmol m^{-2} s^{-1}, Photosynthetic Active Radiation) range. This is because the model describes only the biochemistry of photosynthesis, taking no account of CO_2 transfer from the atmosphere to the site of carboxylation. Other attempts have been made to find adequate mathematical models to describe the PLR curve. Using a general asymptote, Peat [8] was able to obtain a more accurate description of the PLR curve of tomato plants, as did Biscoe *et al*. [9] using barley plants.

A non-linear (called also, non-rectangular hyperbola) model was derived by Thornley [5] who realised that the actual PLR curve was better described by a quadratic model with three parameters, P_{gmax}, α and θ, where θ is a term that governs the '*convexity*' of the PLR curve (see materials & methods). When set at the limit, where θ = 0, the response degenerates into the linear or rectangular hyperbola model [1], but at the other limit, where θ = 1, the response becomes a Blackman-type curve [1]. This model combines a simplified description of the biochemical reactions occurring within the chloroplasts with the physical diffusion of CO_2 from the stomata to the chloroplasts. Marshall and Biscoe [7] later extended this model to include estimates of dark respiration rate and therefore net photosynthesis *Pn*.

In this model, α, the initial slope, is the quantum efficiency at low irradiance, θ is the ratio of physical-to-total resistance (carboxylation resistance r_x + physical resistance r_p), also called the convexity or rate of bending of the PLR curve; P_{gmax} is the maximum rate of gross photosynthesis.

The objective of the present study is to investigate how the measured photosynthetic light-response curve in *Caloropis procera* plants fits under salinity or water stress, to the non-linear model described by Thornley [5] and that derived by Marshall & Biscoe [7].

2. Materials & Methods

2.1. Plant Materials and Growth Conditions

Caloropis procera seeds were collected, pre-germinated and sown according to Akhkha [10]. After pre-germination, seeds were planted in plastic pots filled with compost and sand (3v:1v) then placed in a growth cabinet at a temperature of 28 ± 2ºC, 12 hours photoperiod and 40 ± 5ºC humidity.

2.2. Salinity and water deficit Treatments

Plants were either treated by different NaCl concentrations (150 mmol and 300 mmol) or by different water deficit regimes (50% as mild stress and 30% as severe stress). The 80% of field capacity with 0 mmol NaCl was used as a control.

2.3. Gas exchange measurements

Photosynthetic light-response curves of treated and non-treated Calotropis plants were produced using a Li-cor infra red gas analyser IRGA (LICOR Inc., Lincoln, NE, USA). Photosynthetic active radiations intensities were as follows: 0, 100, 150, 500, 1000 and 1500 μmol quanta m^{-2} s^{-1}. CO_2 concentration was kept as that of the ambient air approximately 370-400 μmol mol^{-1}.

2.4. Data handling and analyses

There are a number of models that can describe the photosynthetic light-response curve PLR such as the Blachman model [1], the linear model or rectangular hyperbola [2] and the non-linear model [5].

In the present study, the non-linear model of Thornley was used with the proposed extension by Marshall and Biscoe [7] which takes in consideration the rate of dark respiration.

Thornley's model:

$$\theta . P^2 - (P_{\max} + \alpha . I) . P + \alpha . I . P_{\max} = 0$$

Marshall & Biscoe [7] extended this non-linear model to include dark respiration *Rd* as follows:

$$\theta . P^2 n - (Pg_{\max} + \alpha . I - \theta . Rd) Pn + \alpha . I . Pg_{\max} - (1 - \theta) Rd . Pg_{\max} = 0$$

The above model was used to estimate the following photosynthetic parameters related to the photosynthetic light-response curve:

P_{gmax}: maximum gross photosynthesis at light saturation

Pn: Net Photosynthesis

P_{max}: Maximum net or gross photosynthesis at light saturation

α: Apparent quantum efficiency

θ: Convexity of the curve

I: Photosynthetic active radiation

Rd: Dark respiration

The non-linear Solver routine in Microsoft Excel 2003 was used to model the light-response curves and calculate the values of P_{gmax}, α, θ and *Rd* [4].

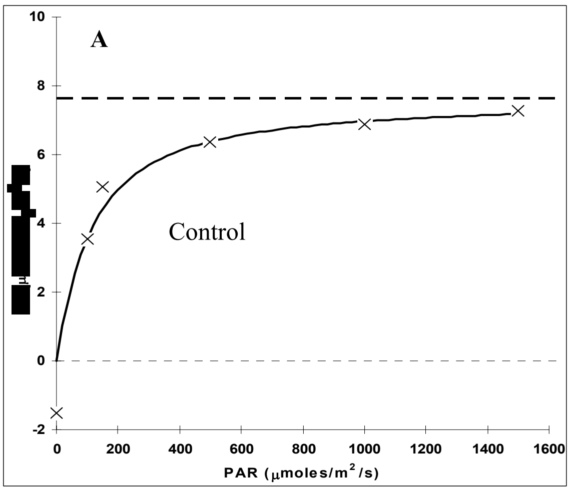
Analysis of variance (ANOVA) was performed on all the data using *General Linear Model* (*GLM*) of the statistical package Minitab (version 15). The values presented are the means of at least three replicates.

3.Results & Discussion

3.1.Photosynthetic light-response curves PLR

Results showed that under control conditions the photosynthetic light-response curve (Fig. 1A) fits very well with the non-linear model described by Marshal and Biscoe [7]. However, the rate of dark respiration was forced by the model to be null. This suggests that PLC of *C. procera* degenerates to Thornley model which underestimate dark respiration to be null.

Under mild (Fig. 1B) or severe (Fig. 1C) water deficit regimes 50% and 30% respectively, the PLR curve still fits well to Thornley model again underestimating dark respiration. The same observation was noted when plants were under mild (Fig. 1D) and severe (Fig. 1E) salinity stress, 150 and 300 mmol NaCl, respectively. This suggests that despite the environmental factors exerted on plants, the PLC still fits very well to the non-linear model of Thornley rather than the modified non-linear model by Marshall & Biscoe [7]. However, when the measured rate of dark respiration is forced into the non-linear model there was a better fit of the data to the non-linear model derived by Marshall & Biscoe [7]. It was also noted that the rates of maximum gross photosynthesis, apparent quantum efficiency and the convexity of the curve were changed (Fig. 2) compared to those derived from Thornley model (Fig. 1).



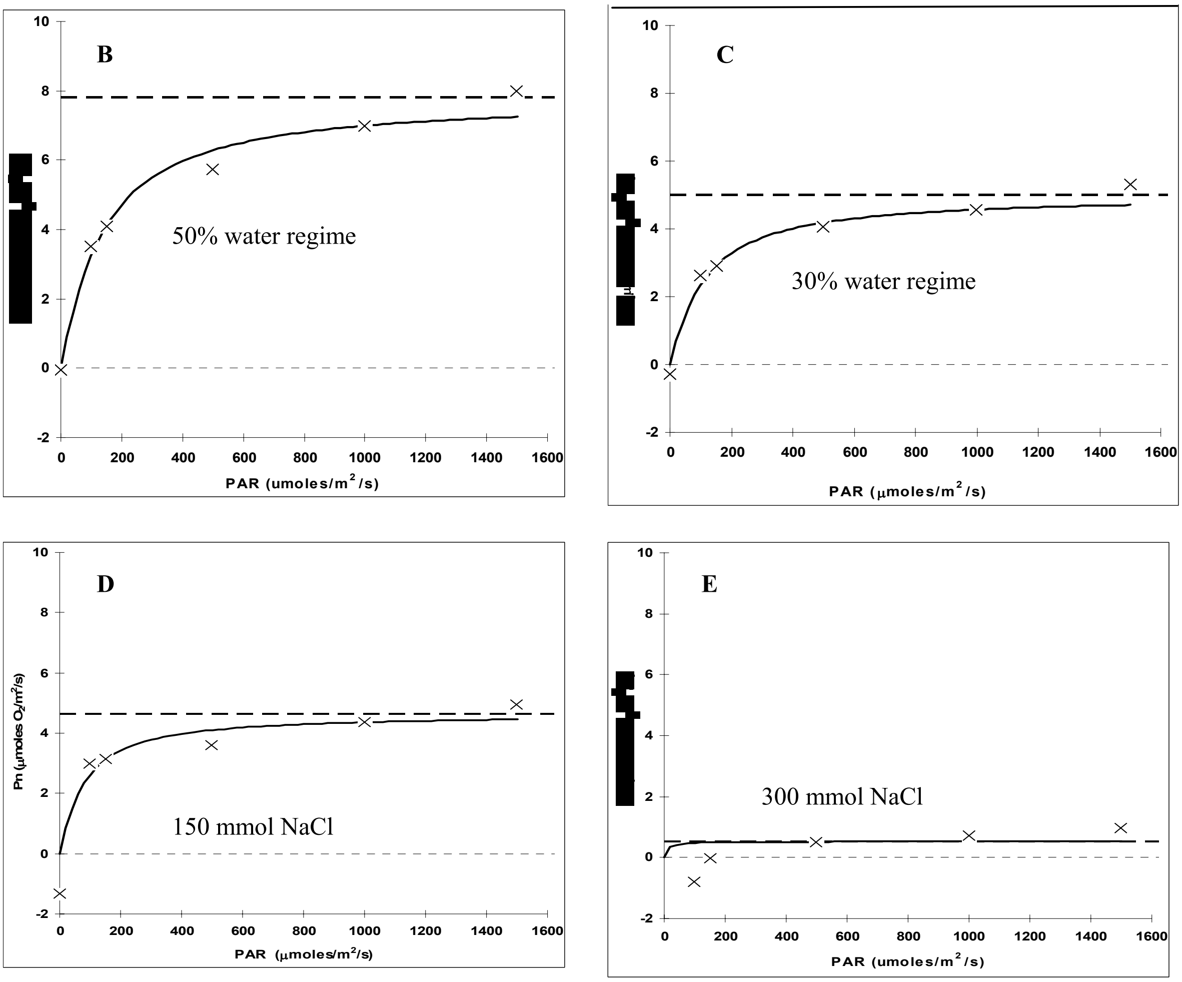


Fig. 1. Photosynthetic light-response curve of control plants (A), plants under water deficit (B = 50% FC and C = 30% FC) and plants under salinity stress (D = 150 mmol NaCl and E = 300 mmol NaCl). Data are fit to the non-linear model, with no constraints on dark respiration values, which degenerates the model to that of Thornley.

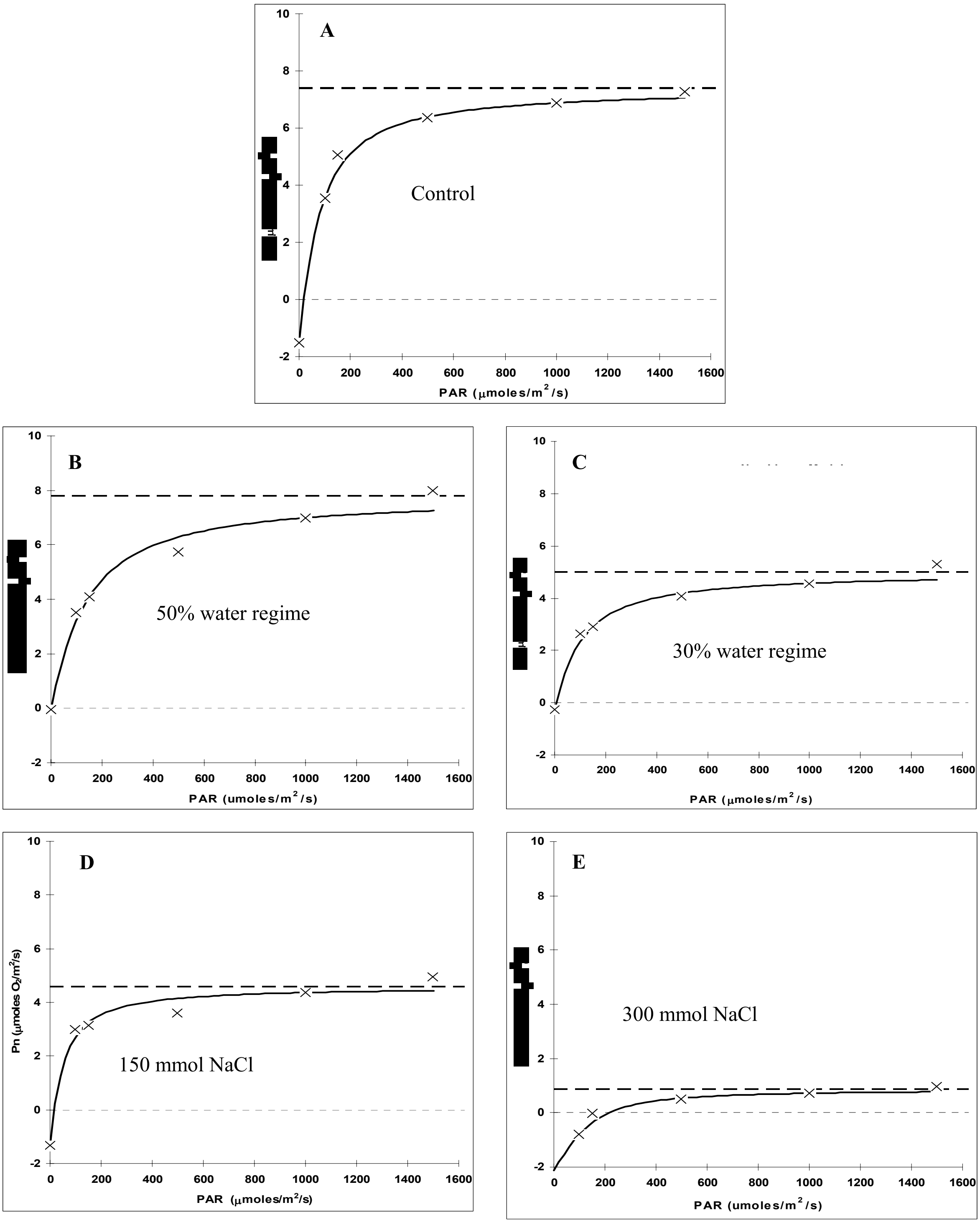


Fig. 2. Photosynthetic light-response curve of control plants (A), plants under water deficit (B = 50% FC and C = 30% FC) and plants under salinity stress (D = 150 mmol NaCl and E = 300 mmol NaCl). Data are fit to the non-linear model, with dark respiration forced to measured values, giving Marshall & Biscoe model.

3.2. Maximum rates of gross photosynthesis P_{gmax}

Although the PLR curve of Calotropis plants under both normal and abnormal environmental conditions followed the non-linear model, the maximum rate of gross photosynthesis P_{gmax} was lowered by the severe water deficit stress (Figs. 3A, 3B) and both mild and severe salinity stress (Figs. 4A, 4B). However, P_{gmax} under severe salinity stress was not too far from zero. It was also noted that P_{gmax} followed the same trend whether it was derived from Thornley's (Figs. 3A, 4A) or Marhsall & Biscoe's model (Figs. 3B, 4B).

3.3. Apparent quantum efficiency α

The apparent quantum efficiency or the initial slope of the PLR curve is a measure of the photosynthetic efficiency of photosynthesis at low light intensities [7]. Using Thornley model at $Rd = 0$, results showed that the efficiency of photosynthesis was decreased gradually as the water deficit (Fig. 5A) or salinity stress (Fig. 6A) increases. Such decrease was explained by Zhu *et al*. [10] as a photoprotection mechanism, which is triggered due to competition between thermal dissipation after receiving photosynthetic active radiations, and the photochemical reactions within the chloroplasts. Such competition triggers a decrease in the efficiency of light use and consequently lowering photosynthesis. These phenomena were very clear in the present study when Calotropis plants were under environmental stress such as water deficit and salinity. This suggests that photoprotection mechanisms were triggered in Calotropis under such growth conditions. Such decreases were more pronounced when α was generated by the derived Marshall & Biscoe non-linear model under both mild and severe water stress (Fig. 5B). In contrast, under salinity stress α was only decreased at severe salinity level (Fig. 6B). This was due to the fact that when *Rd* was included, Marhsall & Biscoe model gave high values of α in the control plants and those under mild salinity conditions.

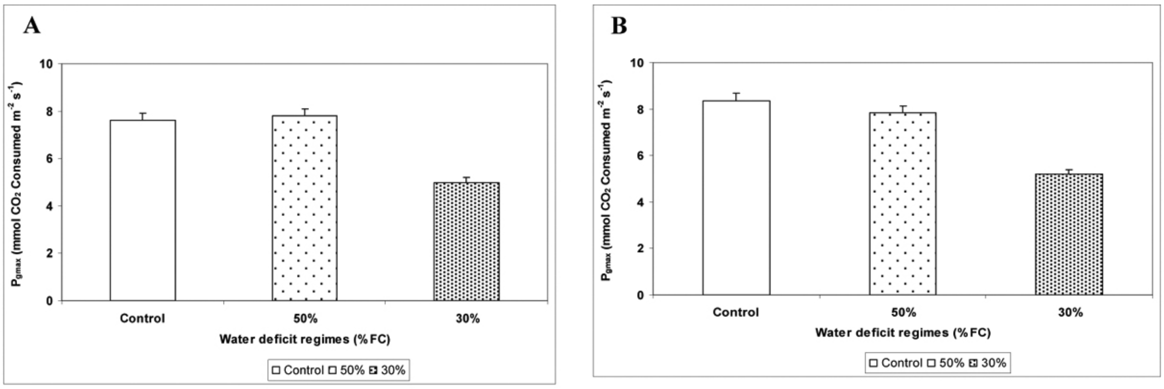


Fig. 3. Maximum gross photosynthesis rate derived from the non-linear model under water deficit. A: Derived from Thornley' non-linear Model; B: Derived from Marshall & Biscoe' non-linear Model.

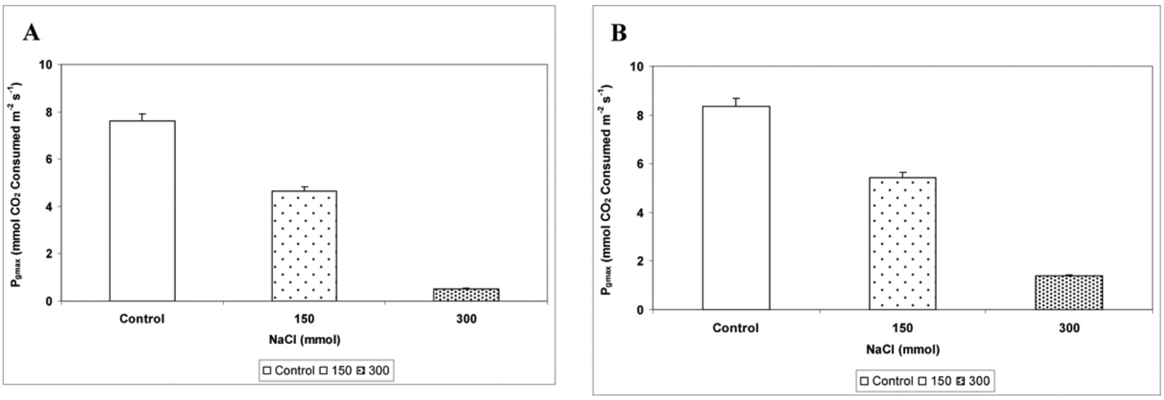


Fig. 4. Maximum gross photosynthesis rate derived from the non-linear model under salinity stress. A: Derived from Thornley' non-linear Model; B: Derived from Marshall & Biscoe' non-linear Model.

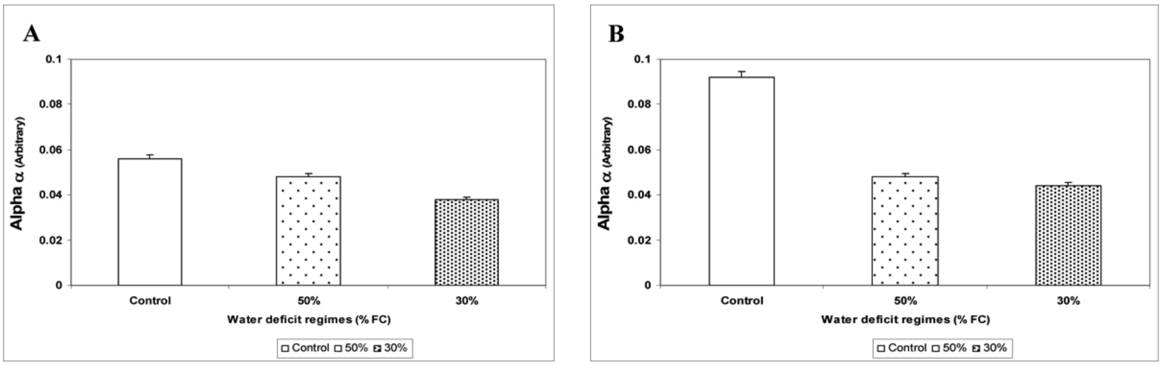


Fig. 5. Apparent quantum efficiency derived from the non-linear model under water deficit. A: Derived from Thornley' non-linear Model; B: Derived from Marshall & Biscoe' non-linear Model.

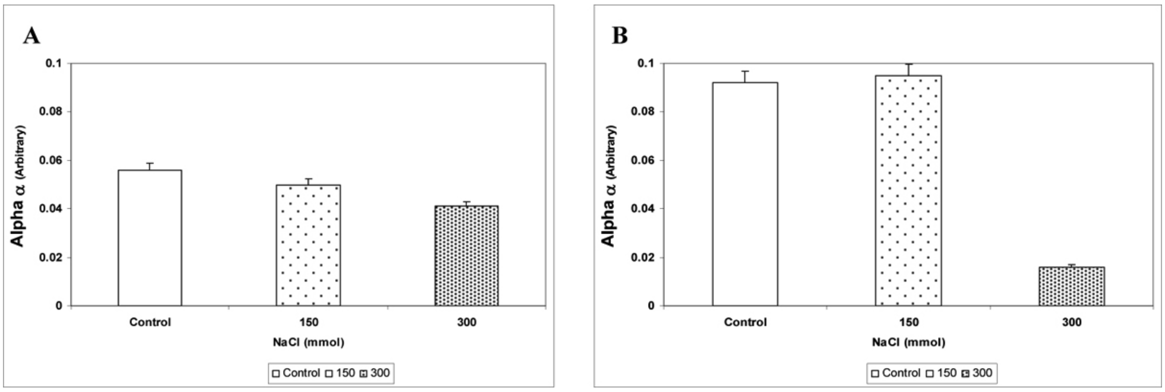


Fig. 6. Apparent quantum efficiency derived from the non-linear model under salinity stress. A: Derived from Thornley' non-linear Model; B: Derived from Marshall & Biscoe' non-linear Model.

3.4. Convexity of the curve θ

The convexity of the curve is an indication of the ratio of physical to total resistance to diffusion of CO_2 into the chloroplasts [12]. The results showed that mild and severe water deficit (Fig. 7A) or salinity stress (Fig. 8A) had no significant ($p > 0.05$) effect on the convexity θ, suggesting that the PLR curve convexity does not change when plants were under either water or salinity stress. However, the values of θ where between 0.335 and 0.306 in all treatments, which suggests that in Calotropis plants under both stress or normal conditions, θ did not change and tends toward the value of zero, which may degenerate the non-linear model of Thorley to the linear or rectangular hyperbola model of Rabinowich with $\theta = 0$. Furthermore, it was expected that θ would decrease in the present study as a photoprotection mechanism against water deficit or salinity stress; this was not the case in Calotropis plants under stress. In contrast, Leverenz *et al*. [13] showed that under photoprotection conditions, θ decreases along with the quantum efficiency [11], and such decrease is very significant to the plants as it increases the light levels at which photosynthesis is depressed [14]. However, when *Rd* was forced into the model, θ was shown to slightly decrease under severe water deficit (Fig. 7B), but significantly increased under severe salinity stress (Fig. 8B). θ value under severe salinity was around 0.8 tending toward 1.0, this is an indication that when Calotropis plants are under severe salinity stress, the PLR curve tends to degenerate to Blackman model (1905) which is characterised by a sharp discontinuity between the light-limited and CO_2-limited regions of the photosynthetic light-response curve. However, this was not the case when Calotropis plants were under severe water deficit, suggesting that environmental factors can affect how data fit different mathematical models. Such observation was reported by Akhkha *et al*. [4] using different plant systems C3 monots, C3 dicots, and C4 plants; the photosynthetic light-response curves followed one model or the other depending on the atmospheric CO_2 conditions used in the experiments.

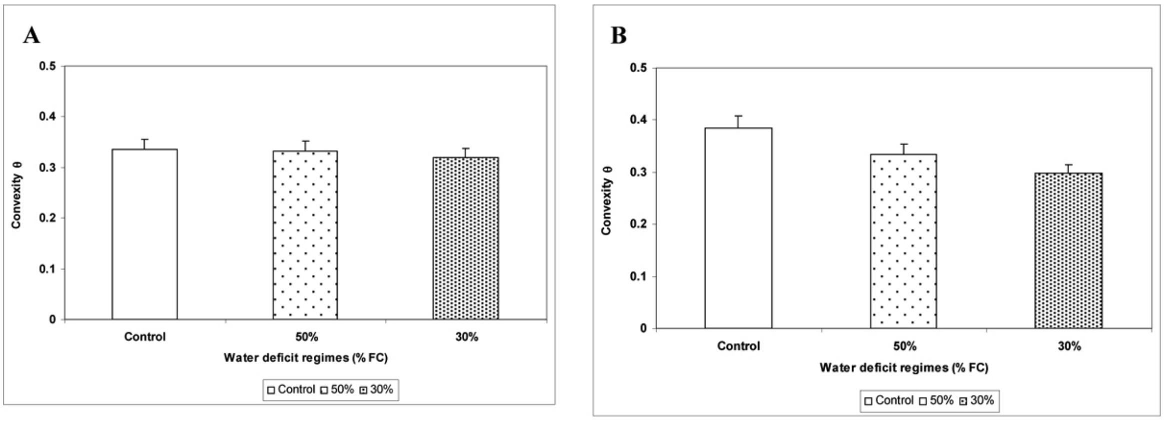


Fig. 7. The convexity of the curve derived from the non-linear model under water deficit. A: Derived from Thornley' non-linear Model; B: Derived from Marshall & Biscoe' non-linear Model.

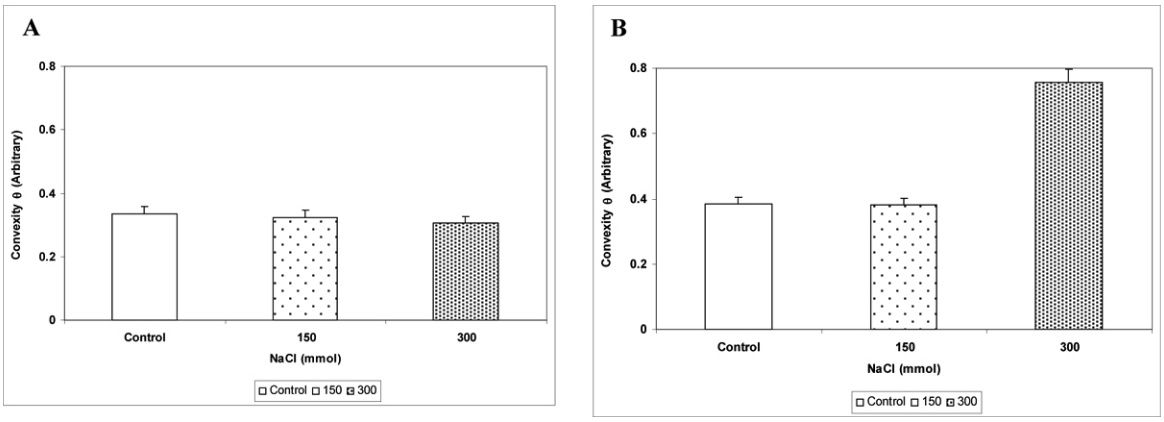


Fig. 8. The convexity of the curve derived from the non-linear model under salinity stress. A: Derived from Thornley' non-linear Model; B: Derived from Marshall & Biscoe' non-linear Model.

4. Conclusion

In the present study, it has been concluded that the photosynthetic light-response curve of Calotropis plants under both normal or stress conditions fits well to Thornley model. Hence, dark respiration was underestimated in this model, generating a value of zero. When the measured dark respiration values were forced into the model, Marshall & Biscoe's model was a better fit. However, this model was degenerated to Blackman model when plants were under severe salinity stress as the convexity tends toward 1. We conclude that under normal and stress conditions Marshall & Biscoe model should be used to estimate photosynthetic light-response curve parameters in Calotropis plants, except at severe salinity stress.

5. References

[1] Blackman, F.F. (1905). Ann. Bot. 19: 281-295.

[2] Rabinowitch, E.I. (1951). Photosynthesis and related processes. Vol. II(1). Wiley Inter Science, New York.

[3] Michaelis, L. and Menten, M.L. (1913). Biochemische Zeitschrift 49: 334-336.

[4] Akhkha, A., Reid, I., Clarke, D.D. and Dominy, P. (2001). Planta 214: 135-141.

[5] Thornley, J.H.M. (1976). *In*: Mathematical models in plant physiology. J. F. Sutcliffe and P. Mahlberg, (Eds.). Academic Press, London, pp. 92-110.

[6] Chartier, P. (1970). In: Prediction and measurement of photosynthetic productivity. A.R. Rees, K.E. Cockshull, D.W. Hand and R.G. Hurd, (Eds.). Academic press, London, pp. 305-326.

[7] Marshall, B. and Biscoe, P.V. (1980). J. Exp. Bot. 31(120): 29-39.

[8] Peat, W.E. (1970). Ann. Bot. 34(2): 319-328.

[9] Biscoe, P.V., Scott, R.K. and Monteith, J.L. (1975). J. Appl. Ecol. 12: 269–293.

[10] Akhkha, A. (2009). Biosci. Biotechnol. Res. Asia 6(2): 653-658.

[11] Zhu, X., Ort, D.R., Whitmarsh, J. and Long, S.P. (2004). J. Exp. Bot. 55: 1167-1175.

[12] Ögren, E. (1993). Plant Physiology 101(3): 1013-1019.

[13] Leverenz, J.W., Falk, S., Pilstrom, C.M. and Samuelsson, G. (1990). Planta 182: 161-168.

[14] Long, S.P., Humphries, S.W. and Falkowski, P.G. (1994). Ann. Rev. Plant Physiol. and Plant Mol. Biol. 45: 633-662.